

# A REVIEW OF THE LATE ORDOVICIAN *FOLIOMENA* BRACHIOPOD FAUNA WITH NEW DATA FROM CHINA, WALES, AND POLAND

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**ABSTRACT.** The late Ordovician *Foliomena* fauna is now known from five palaeocontinents, South China, Avalonia, Baltica, north-west Gondwana, and Laurentia, but has not yet been recorded from the others. New records of the fauna are presented from the Tangtou Formation, South Jiangsu Province, China, and from the *Staurocephalus clavifrons* Beds in Poland, and illustrated for the first time from the Crugan Mudstones of North Wales. The occurrences and ages of all known *Foliomena* faunas are documented and reviewed, and it is concluded that the most typical *Foliomena* fauna, including true *F. folium*, occurred from the latest Caradoc (Onnian) beds to the early upper Ashgill (mid-Rawtheyan). Its ecology is discussed, and evaluated as deep-water, but not necessarily ocean-facing, and marginal to continents. Comparable faunas, one including the closely related ribbed *Proboscisambon*, are identified as occurring in Bohemia, Canada (Percé, Quebec), and Wales (Garth). The taxonomies of *Foliomena* and the *Eoplectodonta* genus-group are briefly discussed, with *Kozłowskites* recognized as a sub-genus of *Eoplectodonta* and *Foliomena* confirmed as a strophomenacean.

KNOWLEDGE of late Ordovician brachiopods has increased enormously during the past quarter century, in particular those faunas which occur peripherally to the main continental cratons or in deeper-water aulacogens within them. One such fauna, a representative of which was monographed for the first time as recently as 1973 (Sheehan 1973), is the *Foliomena* fauna, named after a smooth strophomenacean, which occurs in a distinctive assemblage with other brachiopods listed below. Because trilobites, ostracods, and other animals are sometimes dominantly associated with this fauna, it is not termed here a 'community', since it often forms only a small proportion of the total fossils found, and it is also uncertain how many of the other fauna were benthic and associated with the brachiopods: some of the trilobites, for example, were almost certainly mesopelagic. The brachiopods of the *Foliomena* fauna are all of very small size, are thin-shelled, and never occur very abundantly, which is the chief reason for their lack of systematic attention; and moreover, since the marginal sites in which the fauna often occurs have usually been structurally deformed, the fauna has seldom been systematically collected. However, the fauna, and a related one containing *Proboscisambon* instead of *Foliomena*, have been recognized from various places, and a review is now timely.

## DISTRIBUTION OF *FOLIOMENA* FAUNAS (TABLE 1)

### 1. South China (text-fig. 1)

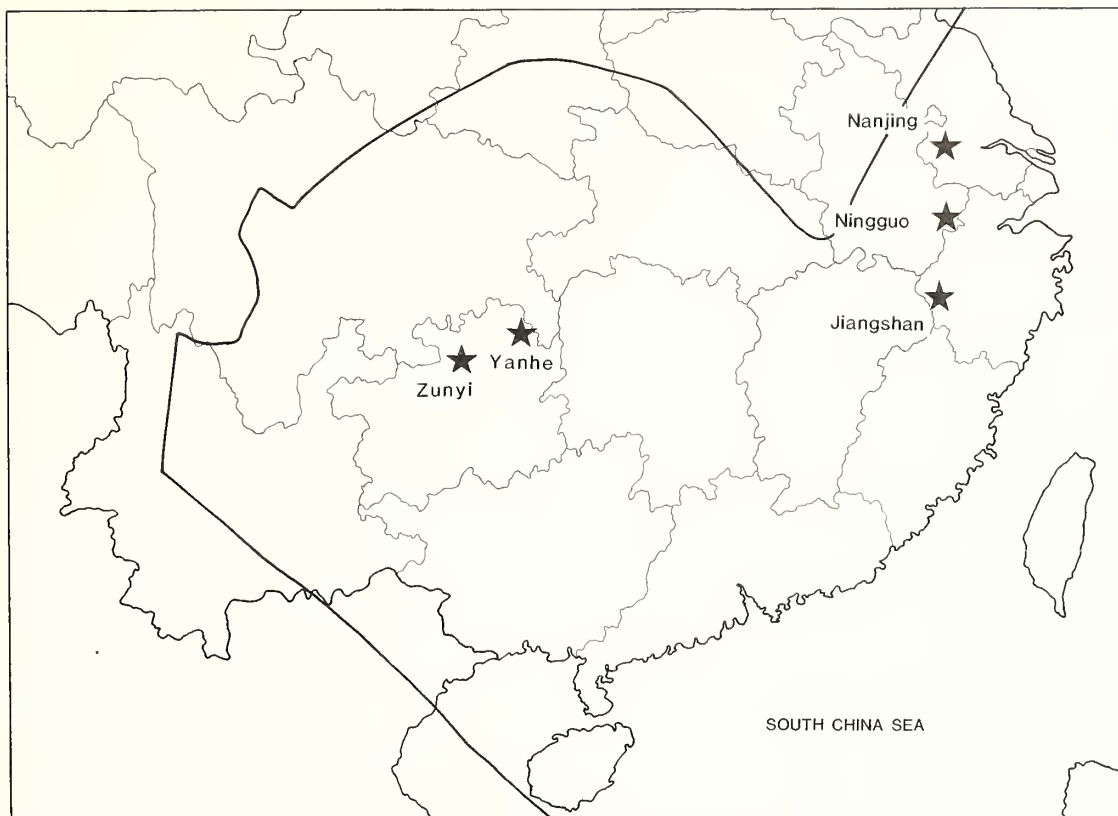
(a) North Guizhou. Mu En-zhi, Zhu Zhao-ling, and Rong Jia-yu collected a *Foliomena* fauna in 1972 from the Linhsiang Formation at Ganxi, Yanhe County, which overlies the Pagoda Limestone with a *Sinoceras chinense* fauna and underlies the graptolitic Wufeng Formation, and consists of green-yellow calcareous mudstones with a thickness of 3.2 m. Brachiopods are uncommon (Rong 1984) and there were fewer than five specimens each of *F. folium* (Barrande), *Kassinella incerta* (Xu and Rong), *Christiania nilssoni* Sheehan, *Dedzetina* sp., and *Aegiromena* sp. Trilobites dominate the fauna and include *Nankinolithus*, *Trinodus*, *Hammatocnemis*, *Corrugatagnostus*, *Shumardia*, *Ampyx*, *Calymenesum*, and others. The age is pre-*szechuanensis* Zone and thus probably early Ashgill. A small collection including *F. folium*, *K. incerta*, and a lingulid (BC 7320-2) has also been made by R. P. Tripp from the Chiencaokou Formation at its type locality at Jiancaohé, Donggongsi, Zunyi County.

TABLE 1. The constitution of the various collections of the true, restricted *Foliomena* fauna from localities detailed

in the text. The actual numbers of specimens collected are shown where known.

	N. Guizhou	NE Guizhou	S. Jiangsu	S. Anhui	W. Zhejiang	North Wales				Myoch, Girvan	Shalloch, Girvan	Ireland	Jerrestad	Västergötland	Poland	Bohemia
						1	2	3	4							
lingulide indet.	×						×			×						
<i>Phillhedra?</i> sp.			1													
<i>Acrothela?</i> sp.			2													
craniacean										×						
eocramatiid										×						
<i>Orbiculoidea</i> sp.					1											
dolerorthid												1				
exopunctate orthid															1	
<i>Glyptorthis</i> sp.							1					7			4	
<i>Dedzetina</i> sp.		×	1			3	×	×	×	×	×	11			2	×
<i>Heterorthina?</i> sp.												4				
<i>Karlicium karlicum</i>																×
<i>Aegiromena</i> sp.		×														
<i>Kassinella incerta</i>	×	×														
<i>Eoplectodonta</i> ( <i>Kozlowskites</i> )																
<i>nuntius/raqnari</i>			4				×					21			3	
<i>Leptestiina prantli</i>			2			40	×	×	×			23	×		5	×
<i>Leptestiina</i> sp.			2	1												
<i>Durranelia?</i> sp.			1			1										
leptellinid indet.				1								1				
<i>Anoptambonites?</i> sp.						1						3				
<i>Leangella</i> sp.						1										
<i>Anisopleurella</i> sp.								1								
Sericoidea										×		1	8			
plectambonitacean indet.				1									1			
<i>Foliomena folium</i>	×	×	4	5	×	27	×	×	×	×		1	250	×	3	×
<i>Christiania nilssoni</i>		×	5	5	×	37		1	×	×		1	36	×	3	
<i>Eostropheodonta</i> sp.						1		1								
<i>Leptaena</i> sp.								1	1							
<i>Holtedahlina?</i> sp.								1								
<i>Eopholidostrophia</i> sp.								1								
<i>Parastrophinella?</i> sp.				1												
<i>Cyclospira?</i> <i>scanica</i>			1	3				?	?	×	×	1	190		4	
<i>Zygospira?</i> sp.						1										
rhynchonellid indet.			1													

(b) South Jiangsu. The Tangtou Formation in the Nanjing area has yielded the following trilobites of the *N. nankinensis* Zone (Lu and Zhou 1981): *Trinodus*, *Corrugatagnostus*, *Shumardia*, *Telephina*, *Nileus*, *Cyclopyge*, *Bumastus*, *Magydenia*, *Phillipsinella*, *Nankinolithus*, *Dionide*, *Lonchodomas*, *Encrinurella*, *Hammotocnemis*, *Atractopyge*, and *Diacanthaspis*. From this formation at Tangtou, Jiangning County, about 20 km east of Nanjing, R. P. Tripp has collected the following brachiopods, which we identify as *Christiania nilssoni* Sheehan (Pl. 9, fig. 9), *Eoplectodonta* (*Kozlowskites*) *nuntius* (Barrande) (Pl. 9, figs. 2, 3, 5, 6), *F. folium* (Barrande) (Plate 9, fig. 8), *Leptestiina prantli*



TEXT-FIG. 1. Locality map of the *Foliomena* fauna in South China, including the boundaries of the provinces and also the boundary of the South China Plate (after Rong and Chen 1987).

Havlíček, *Leptestiina* sp., *Acrothele*? sp., *Dedzetina*? sp., *Cyclospira*? *scanica* Sheehan, *Philhedra*? sp., *Parastrophinella*? sp., *Durranelia*? sp., indeterminate rhychonellid, and a further indeterminate articulate. The age of this fauna is also early Ashgill, since it lies below *szechuanensis* Zone graptolites and above the *Sinoceras chinense* cephalopod zone.

(c) South Anhui. A *Foliomena* fauna was collected in 1974 from the Huangnehkang Formation at Jiugongmiao, Ningguo County, which overlies the Yenwasha Formation with a *S. chinense* faunas and underlies the graptolitic Wufeng Formation, and consists mainly of yellow mudstones bearing trilobites of the *Nankinolithus* Fauna (Rong 1984). Brachiopods are rare but include *F. folium* (Barrande) (Pl. 9, fig. 7), *Christiania nilssoni* Sheehan, *Cyclospira*? cf. *scanica* Sheehan, *Leptestiina* sp., indeterminate leptellinid, and an indeterminate plectambonitacean. The age is the same as north-east Guizhou.

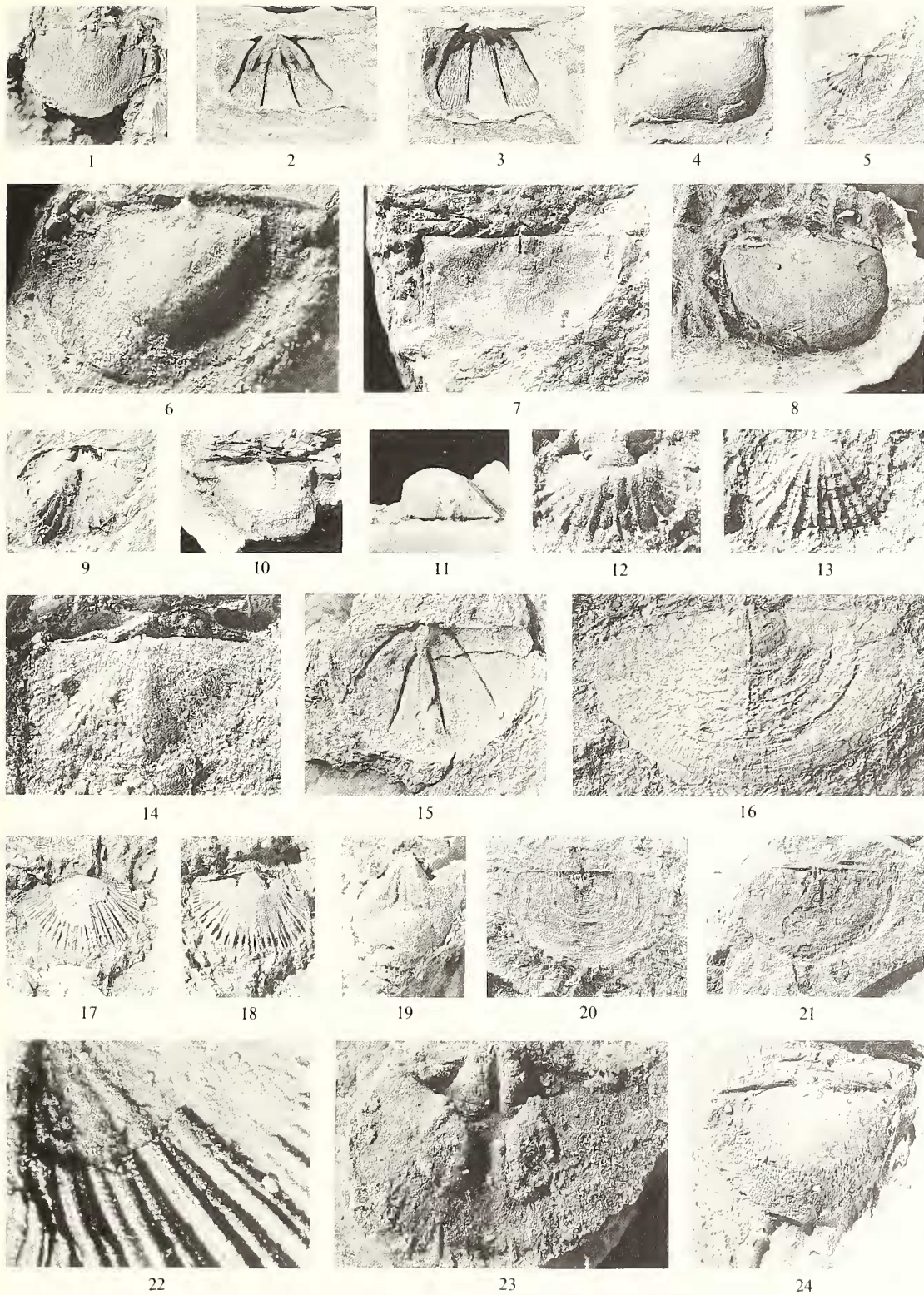
(d) West Zhejiang. The *Foliomena* fauna occurs in two formations in a hill close to the northern border of Jiangshan County, western Zhejiang (text-fig. 1), which was collected by Han Nai-ren. A few specimens from the Huangnehkang Formation of Pusgillian age included *F. folium* (Barrande) (Pl. 9, fig. 14) and *Christiania nilssoni* Sheehan (Rong 1984) (Pl. 9, fig. 10). In addition, a single specimen of *F. folium* was collected from the overlying Changwu Formation, together with five specimens of *Tcherskidium* sp. (Pl. 9, figs. 17–20), four of *Kassinella anisa* Percival (Pl. 9, figs. 11–13, 15), and two each of *Cyclospira*? cf. *scanica* Sheehan and *Leptestiina* sp. from an horizon overlying *szechuanensis* Zone graptolites. This fauna is discussed further in the section on ecology below.

## 2. Wales and Belgium (*Avalonia*)

(a) North-west Wales. In the Llyn Peninsula of western North Wales (Gwynedd) the Crugan Mudstone Formation outcrops in two geographically separated areas (Price 1981), and the *Foliomena* fauna has been collected from the following localities within the formation, chiefly by S. F. Morris, B. Roberts, and D. Price: 1, a road-side quarry in Crugan Lane, 1 km north-east of Llanbedrog, Grid Ref. SH 33323241; 2, a temporary exposure in Dynana farmyard, 1 km north-north-east of Llanystumdwy, SH 481396; 3, an exposure at Berllan Cottage, 1 km north of Llanbedrog, SH 32483365; and 4, section along Afon Penfhos, north-east of Llanbedrog, SH 33503245. The fauna from Locality 1 has been listed by Cocks (in Price 1981, p. 203) as numerous *L. prantli* (Havlicek); *Christiania nilssoni* Sheehan (Pl. 8, figs. 2–4); *F. folium* (Barrande) (Pl. 8, fig. 1); and *Dedzetina* sp.; and one specimen each of *Anoptambonites?* sp., *Eostropheodonta* sp., *Leangella* sp., *Zygospira?* sp., and *Orbiculoidea* sp.; *Durranelia?* sp. (Pl. 8, fig. 5) is also now recorded. Collections from the other localities have also all yielded *Leptestiina prantli*, *F. folium*, and *Dedzetina* sp., with, in addition, *C. nilssoni* and *Leptaena* sp. from Locality 4; *Cyclospira* sp., *Eopholidostrophia* sp., *Leptaena* sp., *Anisopleurella* sp., *Glyptorthis* sp., *Christiania nilssoni*, and *Holtedahlna?* sp. from Locality 3; and *Lingula* sp., another indeterminate lingulide, *Cyclospira* sp., and *Eoplectodonta* sp. from Locality 2. A small locality in the hillside south-east of Locality 2 yielded the first listed record of the *Foliomena* fauna as such (Temple in Roberts 1967, p. 378). The age of the Crugan Mudstone has been determined by Price (1981, p. 206) as fairly high in the Rawtheyan Stage, correlating with Zones 5 to 6 of Ingham (1966).

### EXPLANATION OF PLATE 8

- Figs. 1–11. *Foliomena* fauna from the Crugan Mudstone Formation, North Wales. 1, *F. folium* (Barrande 1879), internal mould of pedicle valve, BB 33232,  $\times 6$ , from roadside quarry in Crugan Lane 1 km north-east of Llanbedrog, Gwynedd, Grid Ref. SH 33343241, collected by S. F. Morris. 2–4, *Christiania nilssoni* Sheehan 1973, internal and external moulds of a brachial valve, fig. 2 taken obliquely to show details of cardinalia, BB 33251,  $\times 3$ , same locality as fig. 1. 5, *Durranelia?* sp., internal mould of brachial valve, BB 33242,  $\times 6$ , same locality. 7 and 8, *F. folium* (Barrande 1879). 7, internal mould of pedicle valve, BB 95938,  $\times 4$ , quarry 150 m west of Crugan Farm, 1 km north-west of Llanbedrog, Gwynedd, Grid Ref. SH 33323241, collected D. Price; 8, latex cast of external mould of pedicle valve showing the unique specimen with a single median costella, BB 33196,  $\times 8$ , exposure at Berllan Cottage, north of Llanbedrog, Gwynedd, Grid Ref. SH 32483365. 9, *Dedzetina* sp., internal mould of brachial valve, BB 33167,  $\times 6$ , temporary exposure in Dynana farmyard, 1 km north-north-east of Llanystumdwy, Gwynedd, Grid Ref. SH 481396, collected by S. F. Morris. 6, 10, 11, *Leptestiina prantli* (Havlicek 1952). 6, internal mould of pedicle valve, BB 33224,  $\times 8$  from Afon Penfhos, 1.3 km east of Llanbedrog Church, Gwynedd, Grid Ref. SH 33503245; 10 and 11, two views of internal mould of pedicle valve, BB 33248,  $\times 4$ , same locality as fig. 1.
- Figs. 14 and 15. *Foliomena* fauna from the Slade and Redhill Mudstone Formation, South Wales. 14, *Aegironetes* sp., internal mould of pedicle valve, BB 26136,  $\times 12$ , from quarry 50 m south of Ruddaxton Church, Dyfed, Grid Ref. SM 961206. 15, *C. nilssoni* Sheehan 1973, internal mould of brachial valve, BB 26687,  $\times 6$ , from Prendergast Place Quarry, Haverfordwest, Dyfed, Grid Ref. SM 956166.
- Fig. 16. *Proboscisambon quaesitus* (Barrande 1879), internal mould of a pedicle valve, MM 039,  $\times 6$ , from *Cryptolithus kosoviensis* horizon, Králův Dvůr Formation, foot of Kosov hill, near Králův Dvůr, Czechoslovakia, collected by M. Mergl.
- Figs. 12, 13, 17–24. *Foliomena* fauna from the *Staurocephalus clavifrons* Bed, Wólka, near Nowa Stupia, Holy Cross Mountains, Poland, collected by W. T. Dean. 12 and 13, *Glyptorthis* sp., internal and external moulds of pedicle valve, BC 7165,  $\times 8$ . 17, 18, 22, exopunctate orthid gen. et sp. indet.; 17 and 18, internal mould and latex cast of the external mould of a pedicle valve, BC 7157,  $\times 4$ ; 22, enlargement of the external mould of the same valve,  $\times 20$ , to show the exopunctate ornament. 19, *Cyclospira* sp., internal mould of pedicle valve, BC 7169,  $\times 8$ . 20 and 21, *Foliomena folium* (Barrande 1879), external and internal moulds of a brachial valve, BC 7177,  $\times 4$ . 23, *Glyptorthis* sp., internal mould of a brachial valve, BC 7163,  $\times 8$ . 24, *Leptestiina prantli* (Havlicek 1952), internal mould of a pedicle valve, BC 7171,  $\times 4$ .



COCKS and RONG, late Ordovician brachiopods

(b) South-central Wales. In the Garth district, Powys, Williams and Wright (1981) have recorded a *Foliomena* fauna from unnamed siltstones of Rawtheyan age (Zones 6 to 7 of Ingham) based on trilobites. From Cwm Clyd Quarry (Grid Ref. SN 946509), they have collected a sparse but diverse fauna which they identified as *Leptestiina* sp., *Cyclospira* sp., plectambonitacean, dalmanellid, *Dedzetina* sp., *Leangella* sp., *Dalmanella* cf. *sculpta* (Cooper, 1956), *Eoplectodonta* sp., ?*Leptestiina*, leptestiinid nov., *Kozlowskites* sp., *F.* cf. *joliensis* Sheehan & Lespérance, *Eospirigerina* sp., *Trimurellina* sp., *Onniella* sp., *Cremnorthis* sp. nov., *Orthambonites?* sp., *Plaesiomys* cf. *porcata* (M'Coy), *Aegiomena* sp. nov., *Chonetoidea* sp., *Leangella* cf. *scissa* (Davidson), leptestiinid, sowerbyellid?, *Gunnarella?*, *Leptaena rugosa* Dalman, *Christiania* sp., strophomenacean, spire-bearer indet., and articulate indet., a total list of twenty-nine species out of only eighty-two specimens. However, as mentioned in the section on ecology below, this fauna does not fall within the range of a typical *Foliomena* fauna, even though *F.* cf. *joliensis* is recorded from it.

(c) Belgium. Passing references to a *Foliomena* fauna in Belgium have been made by Sheehan (e.g. 1979, p. 69), but no details, locality, or age have been published.

### 3. Scotland, Ireland, and Canada (southern margin of Laurentia)

(a) Western Scotland. Harper (1979, 1984) has recorded a *Foliomena* fauna from the red mudstone member of the Myoch Formation, in the upper part of the Whitehouse Group of Girvan, Strathclyde, from five separate localities all within 100 m of each other on the Whitehouse foreshore, south-west of Girvan (Grid Ref. NX 175954 to 176955). Harper (1979, p. 440) provisionally recorded *Lingula*, *Dedzetina*, *Sericoidea*, *Foliomena*, *Christiania*, *Cyclospira*, a craniacean, and a new genus of eocramatiid. The associated trilobites and graptolites indicate an age which lies within the latest Onnian Stage of the Caradoc (Harper 1984, p. 3). Harper (1984) has redescribed *Lingula* sp. and craniid gen. et. sp. indet. 1, but the remainder of the fauna will appear in later parts of his monograph. It is of importance as being the oldest known *Foliomena* fauna, and indeed the only one of probable Caradoc age. Harper (1979, p. 441) also recorded a small fauna from the overlying Shalloch Formation of Cautleyan age in green shales associated with *Dicellograptus anceps* itself and consisting only of *Dedzetina* sp. and *Cyclospira* sp.: he regarded this fauna as a restricted *Foliomena* fauna, and we agree.

(b) Ireland. Harper (1980) recorded and illustrated *Dedzetina* sp., *Sericoidea* sp., *Foliomena* sp., *Christiania* sp., *Cyclospira* sp., and a leptellinid gen. et sp. indet. from the Ballyvorgal Group at Slieve Bernagh, County Clare, but he informs us (pers. comm. 1986) that only one specimen of each taxon was found. Unfortunately there are no other stratigraphically significant fossils known from these beds.

(c) Canada. Sheehan and Lespérance (1978) described a *Foliomena* fauna from the base of the sea cliffs at Mount Joli, Percé, Quebec Province, which at that time they attributed to the White Head Formation, but which Skidmore and Lespérance (1981, p. 40) later excluded from the White Head Formation and simply placed within the Matapediá Group. They list the brachiopods *Lingulacid* gen. et sp. indet., orthacean fam. gen. et sp. indet., dalmanellacid gen. et sp. indet., plectambonitacean fam. gen. et sp. indet., ?*Diambonia septata* (Cooper 1930), *F. joliensis* Sheehan and Lespérance, and *C.?* *minuscule* Cooper 1930, as well as 205 specimens of trilobite attributable to seven species, and 'common' crinoid columnals. The trilobites indicate an age of somewhere within the Ashgill.

### 4. Scandinavia and Poland (Baltica)

(a) South Sweden. The first proper description of any *Foliomena* fauna as such was by Sheehan (1973) from the Jerrestad Mudstone in the Koängen borehole, near Fagelsang, east of Lund, Scania, where elements of the fauna were found in different proportions through 13 m of core. The fauna is dominated by *F. folium* (Barrande) and *C.?* *scanica* Sheehan, and also contained *Christiania nilssoni* Sheehan, *Leptestiina prantli* Havlíček; *Eoplectodonta* (*Kozlowskites*) *ragnari* Sheehan, *Dedzetina* sp., *Sericoidea* sp., *Glyptorthis* sp., *Heterorthina?* sp., *Anoptambonites* sp., and indeterminate dolerorthid, and Aegiomeninae. Associated trilobites and graptolites give the age as within the *complanatus*

graptolite zone and the *Tretaspis granulata* trilobite zone, which is Purgillian. Nilsson (1979) recorded the fauna from the same formation in a borehole 850 m north of Södra Sandby Church, western Scania, and which consisted of *F. folium* (Barrande), *D.?* cf. *honorata* (Barrande), and 'some indeterminable specimens and a couple of orthids and strophomenids' (Nilsson 1979, p. 11). However, these occurred in the *Staurocephalus clavifrons* Zone, which is of Rawtheyan age, and hence younger than the fauna described by Sheehan (1973).

(b) Västergötland, Sweden. Jaanusson (*in* Sheehan 1979, p. 69) records *Foliomena*, *Leptestiina*, and *Christiania* from the Jonstorp Mudstones in Västergötland, and we here confirm the identification of *F. folium* (Barrande) on two specimens (Stockholm Riksmuseet Br 10402 and Br 10625) from the Red Jonstorp Mudstone at Mösseberg, of probable Cautleyan age. Jaanusson (1982, pp. 173–174) also recorded a fauna from the middle beds of the Ulunda Formation in the *Phillipsinella parabola* trilobite zone, which is also probably of Cautleyan age, and includes *F. folium* (Barrande), *Rugosowerbyella rosettana* (Henningsmoen), and *C. nilssoni* Sheehan. Finally, there is a single specimen, Br. 134001, from a limestone in the base of the *Dalmanitina* Beds, and therefore perhaps of early Hirnantian age, from Kullberg, Västergötland, which has four or five primary costellae and definitely no parvicostellae, and which we can thus identify only as *Foliomena?* sp.

(c) Poland. A hitherto unrecorded occurrence of the *Foliomena* fauna is from the *S. clavifrons* Bed at Wólka, near Nowa Stupia, in the Holy Cross Mountains, Poland, where a small number of blocks originally collected by W. T. Dean in 1961 has yielded to us the following brachiopods: *L. prantli* Havlíček (Pl. 8, fig. 24), *Cyclospira?* *agnari* Sheehan (Pl. 8, fig. 19), *Glyptorthis* sp. (Pl. 8, figs. 12, 13, 23), *Christiania nilssoni* Sheehan, *F. folium* (Barrande) (Pl. 8, figs. 20 and 21), *Foliomena?* sp., exopunctate orthid (Pl. 8, figs. 17, 18, 22), *Eoplectodonta* sp., and *Dedzetina* sp. The *S. clavifrons* Beds are Rawtheyan in age (Kielan 1960).

#### 5. Czechoslovakia (north-west Gondwana)

Havlíček & Vanek (1966) described a *Foliomena* fauna from an old (now lost) locality within Prague from the upper part of the Králův Dvůr Formation, 15–20 m under the base of the Kosov Formation, in compact grey-green micaceous shales of the *T. seticornis* horizon, of *anceps* Zone age. They recorded *F. folium* (Barrande), *L. prantli* Havlíček, *D. macrostomoides* Havlíček, and *Karlicium karlicium* Havlíček (see Havlíček 1982, p. 126). A further related fauna from the uppermost Králův Dvůr Formation and containing *Proboscisambon quaesitus* (Barrande) is discussed below in the section on ecology.

### AGE OF THE *FOLIOMENA* FAUNA

In South China the Linhsiang, Huangnehkang, and Tangtou Formations, all bearing the true *Foliomena* fauna, all lie above the Pagoda or Yenwashan Limestone bearing the *Sinoceras chinense* nautiloid fauna and below the Wufeng Shale, which carries a *Dicellograptus szechuanensis* graptolite zone fauna at its base. These formations were correlated with the Shikoan Stage (Sh 1) or late Caradoc, but have been reassigned to the early Ashgill (Purgillian or early Cautleyan) because they immediately underlie the *szechuanensis* Zone, which is usually correlated with the lower to middle *anceps* Zone (Rong 1984). Thus the *Foliomena* fauna is only known from the early Ashgill of China, apart from the specimen of *F. folium* itself from the Changwu Formation of West Zhejiang, which is of Middle Ashgill age.

In Avalonia, the only locality with an accurately dateable true *Foliomena* fauna is within the Crugan Mudstone of North Wales, which Price (1981) had dated as lower Rawtheyan on the basis of the associated trilobite fauna; the other Welsh fauna, that from Garth (Williams and Wright 1981), although accurately dated as mid-Rawtheyan, is one of the closely comparable faunas containing *F.?* cf. *joliensis* rather than *F. folium*. The Belgian occurrence has not yet been dated. From Baltica, which was at least in close faunal contact with Avalonia at the time (Cocks and Fortey 1982), and may even have collided with it, the *Foliomena* fauna is known from both the Purgillian/Cautleyan and also the Rawtheyan in Scania, south Sweden, and from the Middle Ashgill in Västergötland, central

Sweden, the Rawtheyan horizon in Scania is from the *Staurocephalus clavifrons* trilobite zone, in which the *Foliomena* fauna also occurs in the new fauna from the Holy Cross Mountains, Poland, near the southern margin of the palaeocontinent. From the north-western margin of Gondwana, the *Foliomena* fauna is known only from the upper part of the Králův Dvůr Formation of Bohemia, which lies within the *anceps* Zone, and is probably of Rawtheyan age (Havlíček 1982).

From Laurentia, the best record comes from the Myoch Formation of Girvan, which correlates with the upper part of the *linearis* Zone and probably with the late Onnian stage of the Caradoc (Harper 1984). The correlation is also based on the occurrence of *T. ceriodes* from the basal beds of the Upper Whitehouse Group (Ingham 1978), suggesting that the early and middle *linearis* Zone is no younger than Onnian in age (Williams and Bruton 1983). A restricted *Foliomena* fauna also occurs in the overlying Shalloch Formation of *anceps* Zone age, which may be early Cautleyan (Harper 1979). Along strike, at Percé, Canada, the previously reported *Foliomena* fauna of Sheehan and Lespérance (1978) cannot be dated exactly within the Ashgill.

To sum up, the age of the *Foliomena* fauna mainly falls within the Puzgillian, Cautleyan, and early to middle Rawtheyan, with a single fauna from Girvan being perhaps of late Caradoc (Onnian) age. The comparable *Proboscisambon* fauna is only known undoubtedly from Rawtheyan rocks, and all the occurrences of both faunas appear to be stratigraphically older than the *Hirnantia* faunas of the latest Ordovician (text-fig. 2).

#### ECOLOGY OF THE *FOLIOMENA* FAUNA

Without exception, all the known occurrences of the *Foliomena* fauna are in fine-grained rocks, usually fine mudstones. In addition, all of the brachiopods are small, with very few specimens over 10 mm in width. They are also invariably very sparsely distributed in low density through the sediment, and this latter fact has also meant that the sample sizes of the collections available both to us and to other workers have very often been pitifully small. This collecting failure exacerbates the problem of comparing the relative diversities of the various collections of brachiopods. Brachiopods

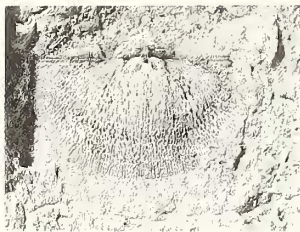
#### EXPLANATION OF PLATE 9

- Figs. 1 and 4. *Foliomena* fauna from Chiencaokou Formation, Donggongsi, Zunyi City, West Guizhou Province, China, collected by R. P. Tripp. 1, *Foliomena folium* (Barrande 1879), internal mould of pedicle valve, BC 7426,  $\times 4$ ; 4, *Kassinella incerta* (Xu, Rong and Liu 1974), internal mould of pedicle valve, BC 7424,  $\times 4$ .
- Figs. 2, 3, 5, 6, 8, 9. *Foliomena* fauna from Tangtou Formation, Lunshan trench, 20 km north-east of Nanjing, Jiangsu Province, China, collected by R. P. Tripp. 2, 3, 5, 6, *Eoplectodonta* (*Kozlowskites*) *nuntius* (Barrande 1879). 2 and 6, internal and external moulds of a pedicle valve, BC 7126,  $\times 4$ ; 3, internal mould of brachial valve, BC 7125,  $\times 4$ ; 5, internal mould of small pedicle valve, BC 7148,  $\times 4$ ; 8, *F. folium* (Barrande 1879), internal mould of pedicle valve, BC 7144,  $\times 8$ ; 9, *Christiana nilssoni* Sheehan 1973, internal mould of pedicle valve, BC 7133,  $\times 6$ .
- Fig. 7. *F. folium* (Barrande 1879), from Huangnekang Formation, Jiugongmiao, Ningguo County, South Anhui Province, China, internal mould of pedicle valve, NIGP 101831,  $\times 6$ .
- Figs. 10 and 14. *Foliomena* fauna from Huangnekang Formation, hill to west of Jiangshan County, south-west Zhejiang Province, China. 10, *C. nilssoni* Sheehan 1973, internal mould of pedicle valve, NIGP 101829,  $\times 8$ . 14, *F. folium* (Barrande 1879), internal mould of pedicle valve, NIGP 101830,  $\times 4$ .
- Figs. 11–13, 15–20. Fauna allied to *Foliomena* fauna from Changwu Formation, hill to west of Jiangshan County, south-west Zhejiang Province, China. 11–13, 15, *Kassinella anisa* Percival 1979; 11 and 12, internal moulds of pedicle valves, NIGP 101833 and NIGP 101834,  $\times 4$ ; 13 and 15, internal moulds of brachial valves, NIGP 101835 and NIGP 101836,  $\times 4$ . 16, *F. folium* (Barrande 1879), external mould of conjoined valves, NIGP 101832,  $\times 6$ . 17–20, *Tscherskidium* sp. 17 and 20, internal mould of brachial valve viewed from posteriorly and above, NIGP 101827,  $\times 2$ ; 18 and 19, internal mould of a pedicle valve viewed from above and posteriorly, NIGP 101828,  $\times 2$ .





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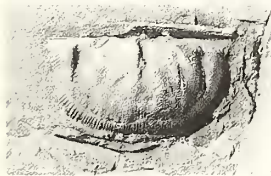
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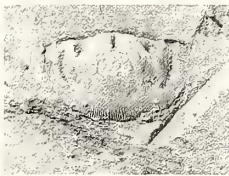
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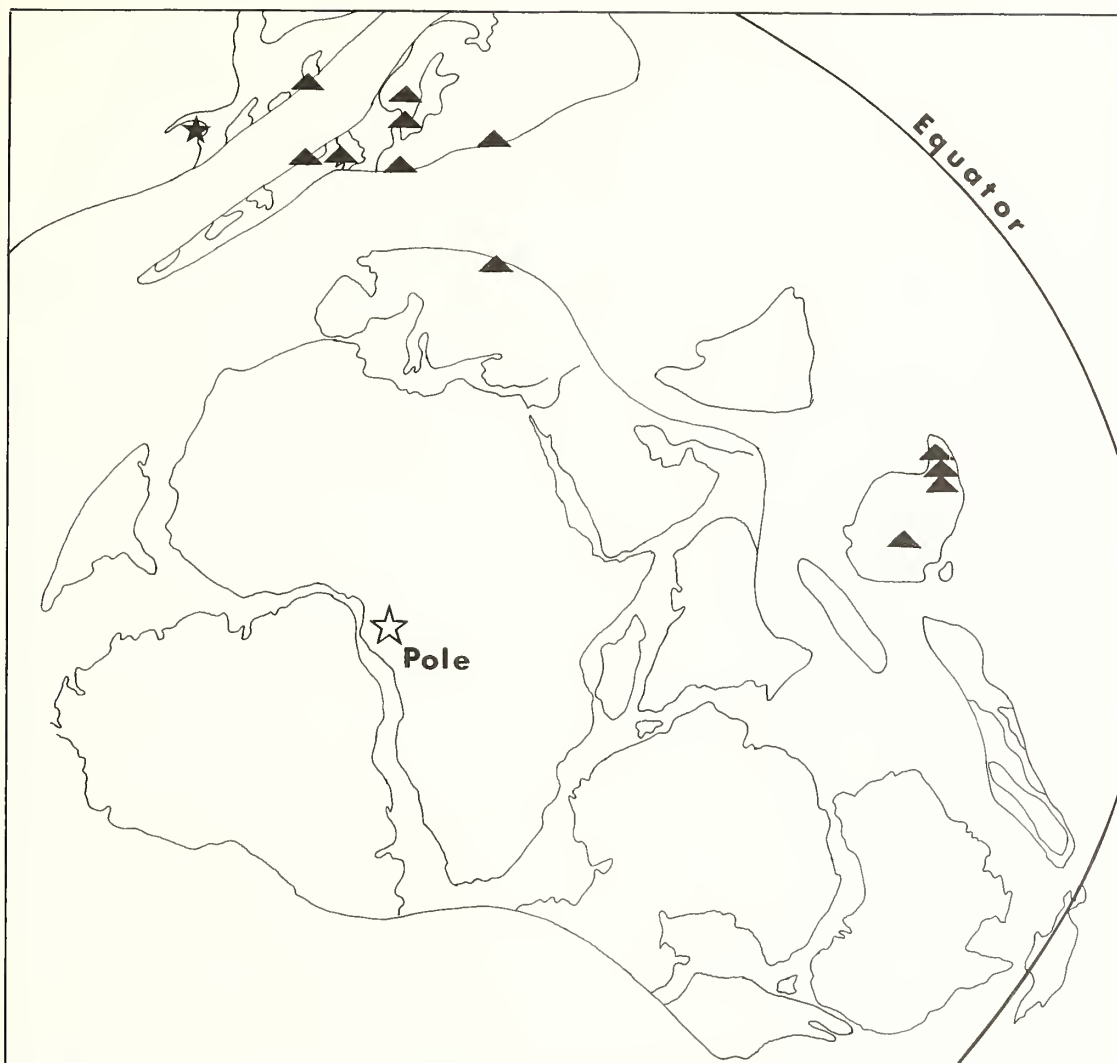
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	European graptolite zones	Chinese graptolite zones	SOUTH CHINA				LLYN PENINS WALES	GARTH WALES	GIRVAN	SCANIA SWEDEN	VÄSTER GÖT LAND	HOLY CROSS MTS.	BOHE MIA
			NE. GUIZHOU	S. JIANGSU	S. ANHUI	W. ZHE JIANG							
RHUDDANIAN	acuminatus	acuminatus	LUNGMA CHI FM	KAOCHIAPIEN FM				LADY BURN FM	Rastrites SHALES	Rastrites SHALES	BARDO BEDS	LITEN FM	
HIRNANTIAN	persculptus	persculptus						WENA FM				KOSOVO FM	
	extraordinarius	A. bohemicus	★	★	★			★ LLT FM	★ HIGH MAINS	Dalmanitina BED	TOM MARP BEDS	Dalmanitina BED	★ 5
RAWTHEYAN	pacificus	P. uniformis D. mirus T. typicus	WUFENG FM						UN NAMED SILT STONES			Stauriceps clavifrons BED	
	anceps	D. szechuanensis				CHANGWU		CRUGAN MUDSTONE	DRUMMUCK GP				
CAUTLEYAN												P.par. Bed	KRALUV DVUR FM
PUSGILLIAN	complanatus	A. disjunctus yangtzeensis	LIN HSIANG FM	TANG TOU FM									
	linearis				HUANGNE				SHAL LOCH FM				
					KANG FM			UPPER WHITE HOUSE GP				N gran. Bed	
ONNIAN			PAGODA FM		YENWASHAN FM		PENARWEL SHALE	"BALA MUDSTONES"			FJACKA SHALE		BOHDALEC FM

TEXT-FIG. 2. Correlation of the true *Foliomena* fauna (shown by triangles), the *Hirnantia* fauna (shown by stars), and some faunas related to the *Foliomena* fauna, with the European and Chinese graptolite zonation (Williams 1986; Mu *et al.* 1979). The numbers indicate: (1) A shallower brachiopod fauna with *F. folium*, *Kassinella anisa*, and *Tcherskidium* sp., (2) *Foliomena* sp. associated with a high-diversity brachiopod fauna; (3) A fauna allied to the *Foliomena* fauna but with no *F. folium*; (4) *Foliomena?* sp.; (5) *Proboscisambon* with no *Foliomena*. Quebec's data with no precise age, and the Belgian fauna (unpublished) are not included.

very often form only a small proportion of the total fauna, which is commonly dominated by trilobites and sometimes ostracods. All previous workers, e.g. Sheehan (1973), Harper (1980) have considered the fauna to have been deposited under deep-water, and we agree with this analysis, but for additional reasons. First, the fauna is known from five different palaeocontinents in late Ordovician time (text-fig. 3), and moreover continents whose palaeolatitudes differed very considerably (Cocks and Fortey 1988). It has already been stated (e.g. Cocks and Fortey 1982) that the deep-water faunas are the ones most likely to be of a more even temperature, and hence less latitudinally dependent, and so the disparate occurrences of the *Foliomena* fauna in both space and time might be expected from their deeper-water mode of life. This is in contrast with the adjacent shallower-water communities, the occurrence of which reflect continental distributions and palaeolatitudes (Cocks and Fortey 1982, fig. 1). The total biota in which the *Foliomena* fauna is found is dominated by trilobites, very often including the cyclopygids, and this trilobite biofacies is also consistently indicative of a deeper-water habitat (Fortey 1985), which strengthens our conclusions drawn from the brachiopods. However, we agree with Sheehan (1977) that the brachiopod fauna was indigenous to the substrate in which it is found, for the following reasons: (a) a high proportion of shells are found still articulated, which argues against transportation; (b) the *Foliomena* fauna is found consistently together, whereas if it lived epiplanktonically at or near the surface its remains ought to be found scattered more widely and also over a greater range of lithofacies, including shallower ones; and (c) a uniformly smaller and thinner-shelled fauna is more likely to be found in deep rather than shallow water (Fürsich and Hurst 1974). This is not to say that the *Foliomena* fauna depths were very great, and probably not off the continental shelves, as can be seen by its distribution in, for example, south China and Sweden (Västergötland); these areas, although undoubtedly relatively deep, only represented depressions in the continental landmasses.

The other faunas closely related to the *Foliomena* fauna are also relevant here. The first is the so-called *Proboscisambon* Community of Havlíček (1982), which is known only from the uppermost



TEXT-FIG. 3. The distribution of the *Foliomena* fauna during Ashgill times. The palaeogeographic map, which omits Siberia, Kazakhstan, and North China, is taken from Cocks and Fortey (1988).

Králův Dvůr Formation at Kosov Hill, near Králův Dvůr, Zadní Treban, Liten, and Jezerka; all in the Prague area, Czechoslovakia. Like the typical *Foliomena* fauna (which occurs lower down in the same formation: see above), it occurs in calcareous silty shales and contains low-density, high-diversity brachiopods with greater numbers of trilobites and ostracods. The brachiopods include abundant (more than 100 specimens) *P. quaesitus* (Barrande), *Kozłowskites ragnari* Sheehan, *Ravozetina honorata* (Barrande), *R. opima* Havlíček & Mergl, relatively common (50–100 specimens) *Aegironetes tristis* (Barrande) and *Epitomonia dorcicava* Havlíček & Mergl, fewer than 50 specimens of *Durranelia moneta* (Barrande), and rarer specimens of 'Salopina', *Jezercia ostaria* Havlíček & Mergl, *Boticium*, *Cliftonia*, *Leptaena*, *Cryptothyrella*, *Ornothyrella*, and others. True *Foliomena*, *Christiania*, *Leptestiina*, and *Cyclospira* are all absent from that list, but nevertheless it seems probable that the *Proboscisambon* fauna does represent a comparable ecological position to the

*Foliomena* fauna, particularly in view of the 'Foliomena' faunas of Percé, Canada (Sheehan and Lespérance 1978) and Garth, Wales (Williams and Wright 1981), where the place of the smooth *F. folium* itself is taken by the ribbed and closely related *Foliomena?* sp. (although final attribution must await elucidation of the internal features of the Canadian and Welsh forms).

The other fauna is the one listed above from the Changwu Formation of West Zhejiang, China, in which a single (but undoubted) specimen of *Foliomena* and rare *Cyclospira?* and *Leptestiina* occur with *Tscherskidium* and *Kassinella*. This is one of the few places in eastern China where early pentameraceans (*Tscherskidium*) are known from mid-Ashgill rocks; the other is from the Sanjushan Formation of Zhuzhai, Yushan County, north-eastern Jiangxi Province (Rong and Han 1986), where argillaceous limestones bearing *Tscherskidium* are interbedded with coral horizons including abundant *Agetolites*, *Kolymopora*, *Fletcheriella*, *Plasmoporella*, *Heliolites*, and *Stelliporella*, which have also been found in the north-eastern USSR (Yang 1984). *Tscherskidium* itself is characteristic of the Rawtheyan fauna of the north-east USSR (Koren *et al.* 1983) and it has also been doubtfully recorded from the western slope of the northern Urals and southern Kazakhstan (Rukavishnikova and Sapelnikov 1973; Sapelnikov and Rukavishnikova 1975). Another distinctive brachiopod occurring in the Chungwu Formation with *Foliomena* is *Kassinella anisa* Percival, a plectambonitacean hitherto recorded only from New South Wales, Australia (Percival 1979), where it apparently occupied a relatively shallow-water environment. We interpret the Changwu Formation fauna as having lived in medium shelf depths, with the odd record of *Foliomena* as probably representing the extreme shallow end of its depth range.

#### SYSTEMATIC NOTES

Superfamily PLECTAMBONITACEA Jones, 1928

Family SOWERBYELLIDAE Öpik, 1930

EOPLECTODONTA Kozłowski, 1929

*Eoplectodonta* was originally erected as a subgenus of *Plectodonta* by Kozłowski (1929), but has been treated as a separate genus for many years (e.g. Williams *et al.* 1965): the differences between *Eoplectodonta* and *Plectodonta* were tabulated by Cocks (1970, p. 167). Unknown to Kozłowski, *Eoplectodonta* had a long history prior to Silurian times, and is known from rocks at least as old as Llandeilo in age. Various genera have been erected which are very closely related to *Eoplectodonta*, including *Eochonetes*, *Kozłowskites*, and *Thaerodonta* from the late Ordovician. All have denticulate hinge lines, but *Eochonetes* is distinct from the others in possessing, in addition, a perforate hinge line. *Thaerodonta* has been revised by Rõõmusoks (1981), and is not considered further here: of the group, only *Eoplectodonta s.s.* and *Kozłowskites* are known from the *Foliomena* fauna. Havlíček (1952) erected *Kozłowskites* as a separate genus, upon which he elaborated further in 1967, but Williams (in Williams *et al.* 1965, p. H381) regarded it as only a subgenus of *Eoplectodonta*, an opinion followed by Sheehan (1973). Havlíček (1967) listed the chief difference as the absence of the pedicle valve median septum in *Kozłowskites* (although the 'septum' in *Eoplectodonta* is more in the nature of an elongated myophragm between the pedicle valve muscle scars). We follow Williams and Sheehan in considering *Kozłowskites* to be a subgenus of *Eoplectodonta*. Although the two stocks are very closely related, we regard them as more than specifically distinct because (i) since the pedicle opening of *Kozłowskites* is larger, the muscle scars diverge directly from either side of it with a slight space between them, unlike *Eoplectodonta* where they are closer together and separated only by the variably developed myophragm, and (ii) the brachial valve muscle area is relatively shorter (always less than half the valve length) and more likely to be enclosed posteriorly by the bounding ridge in *Kozłowskites* than in *Eoplectodonta* where the scars are always over half the length and almost always open posteriorly.

Although shells in the *Foliomena* fauna are usually rather small, when they are well enough preserved to be identified accurately, they are usually found to be *Eoplectodonta* (*Kozłowskites*) rather than *E.* (*Eoplectodonta*), although contemporary assemblages from shallower palaeodepths (e.g. Cocks 1982) usually contain only *E.* (*Eoplectodonta*).

## Superfamily STROPHOMENACEA King, 1846

## Family FOLIOMENIDAE Williams, 1965

## FOLIOMENA Havlíček, 1952

Since *Foliomena* was proposed (Havlíček 1952), with its monotypic species from the Ashgill Králův Dvůr Formation of Bohemia, only one other species has been assigned to the genus, *F. joliensis* from the Ashgill of Percé, Canada (Lespérance and Sheehan 1978). Another genus, *Proboscisambon*, was established by Havlíček and Mergl (1982), with type species *P. quaesita* (Barrande), a species which Havlíček had previously (1967, p. 36) assigned to the plectambonitacean *Anoptambonites*. Havlíček and Mergl listed *F. joliensis* as a synonym of *P. quaesita* and placed *Proboscisambon* with the Foliomenidae, which Williams (1965) had erected as a monogeneric family within the Strophomenacea.

Various questions have arisen in the course of our work.

(a) *Is Foliomena a plectambonitacean or a strophomenacean?* Havlíček (1952) placed his new genus within the Strophomenacea, and this was followed by Williams (1965) when he elevated the taxon to familial rank. However, Bergström (1968, p. 480) wrote that 'it seems probable that this family ought to be placed in the vicinity of Leptestiidae Öpik within Plectambonitacea rather than within Strophomenacea', and Sheehan (1973, p. 65) followed Bergström's assignment. However, the basic difference between the two superfamilies is the bilobed cardinal process of the Strophomenacea and the trilobed cardinal process of the Plectambonitacea. There is no doubt that the cardinal process of *Foliomena* is bilobed (Havlíček 1952, p. 31; 1967, pl. 9, figs. 2 and 13), and this is confirmed by the examination of our own specimens described in this paper. Thus, the Foliomenidae must be placed within the Strophomenacea.

(b) *What are the differences between Foliomena and Proboscisambon?* The two genera are very similar in shell size, outline, and convexity, in their prominent pedicle sheath, in lacking dental plates, and in the size and proportions of the faintly impressed muscle fields in both valves. However, *Proboscisambon* differs from *Foliomena* in the following ways: (i) it has radial ornamentation of very fine parvicostellae and stronger axial costellae (3–7 in number), in contrast to the smooth shell of *Foliomena*; (ii) it lacks a cardinal process (Havlíček 1982, p. 45), in contrast to the bilobed cardinal process of *Foliomena*; (iii) it lacks any septa in the brachial valve, in contrast to *Foliomena*, which has a prominent pair of slightly divergent septa; and (iv) it has prominent dispersed papillae on the inner surface of the shell, in contrast to *Foliomena* which has very fine and dense papillae almost all over the shell interior. From this, *Foliomena* can be rediagnosed as follows: shell small to medium size, gently concavo-convex, nearly flat; pedicle sheath prominent; ornament only of fine growth lines and occasional rugae; no dental plates; pedicle valve muscle scars faintly impressed and divided by a small myophragm; small bilobed cardinal process; socket plates nearly parallel with hinge line; pair of lateral septa; fine papillae irregularly distributed over most of the internal shell surface.

(c) *Should 'F.' joliensis be placed within Proboscisambon?* There is no doubt that the specimens of *F. joliensis* illustrated by Sheehan and Lespérance (1978, pl. 1, figs. 7–13) have costellae. However, the problem is that in neither case are internal features available, and thus it is not known whether the other very distinctive features of *Proboscisambon* (the lack of cardinal process and of brachial valve septa) are developed in the Canadian shells. It is still possible that *F. joliensis* has all the features of true *Foliomena* apart from the development of costellae and parvicostellae. Thus, we have identified the Canadian specimens as *F.?* *joliensis* until full details of their internal morphology become available. The Garth specimen illustrated as *F. cf. joliensis* by Williams and Wright (1981, fig. 2F) is quite similar to the single specimen, Br 134001, from the base of the *Dalmanitina* Beds at Västergötland: they both have three to five primary costellae and no fine parvicostellae, although their internal details are unknown. They differ from the true *F.?* *joliensis* of Quebec in their lack of fine parvicostellae. In addition, a single one of the many specimens of *F. folium* from the Crugan Mudstones of North Wales (BB 33196; Pl. 8, fig. 8) has a single marked central costella without any sign of fine parvicostellae. It seems to us that this specimen may have been a precursor of the Garth and Västergötland specimens, which we have provisionally identified here as *Foliomena?* sp.

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*Note added in proof.* Since this paper was written, R. A. Fortey has made a collection from a muddy limestone equivalent to the Setul Formation from an outcrop in La Ngu District, Satun Province, south-west Thailand, which contains trilobites of south Chinese aspect and can be dated as certainly close to the Caradoc–Ashgill boundary, and perhaps early Ashgill in age. From this limestone we have identified several specimens of *Foliomena folium* (including some small growth stages) and *Christiania* sp. and rather fewer specimens of *Orbiculoidea* sp. This is the first record of the *Foliomena* fauna from the Burma–Thai–Malaysian Peninsula and adjacent areas.